Reference: *Biol. Bull.*, **136**: 398–404. (June, 1969)

EVIDENCE FOR THE ENDOGENOUS CONTROL OF SWIMMING IN PINK SHRIMP, *PENAEUS DUORARUM*[1]

D. A. HUGHES

Institute of Marine Sciences, University of Miami, Miami, Florida 33149

Most animals habitually exposed to water currents orientate and swim in either an upstream or downstream direction. Changes in physical or chemical conditions may elicit a reversal of this rheotactic response. In a few studies (Beauchamp, 1933, 1937; Keenleyside and Hoar, 1954; Creutzberg, 1961) these reversals have been shown to be adaptive, enabling the movement or displacement of the animal in a direction advantageous to it.

Such reversals have been found in pink shrimp, *Penaeus duoarum,* Burkenroad (Hughes, 1969). Juveniles of this species usually swim actively against a current. However, when salinity is reduced, when the animals are starved, or when the water becomes polluted, the shrimp will turn about and swim downstream, with active swimming often giving way to passive drifting. The normal rheotactic response enables juvenile shrimp to evade inshore displacement by flood tides while the reversal, occurring in response to decreased salinity, enables them to utilize ebb tides to effect offshore movement at an appropriate stage in their life cycle.

During the course of the above study, it became evident that all individuals of a group, maintained within a constant current in the laboratory, would, at any one time, carry out essentially the same type of swimming in terms of its velocity and direction with respect to current. Yet the velocity and direction of swimming of the group as a whole often varied throughout the night, despite the absence of any change in external conditions. This indication of endogenous control over swimming was further investigated.

Apparatus and Methods

The experiments were conducted in two identical ring-shaped "current chambers" constructed of "Plexiglas" and based on the design used by Creutzberg (1961) for his study of migration of elvers. This design has been described and figured elsewhere (Hughes, 1969). The apparatus was housed in a light-tight enclosure in the laboratory and illuminated constantly by a centrally placed 5w red bulb, which provided just enough light to permit observation at night. In addition, a 150 w flood lamp, deflected off the white ceiling, supplied the "daytime" illumination during light cycles which approximated those in nature. The salinity of the water in the chambers was usually between 32 and 34‰. No fluctuations during experiments was possible since the water was circulated through a closed system. Temperature within the laboratory was maintained constant throughout this work. The current speed, maintained at 12 cm/sec, was arbitrarily chosen as one against

[1] Contribution No. 1034 from the Institute of Marine Sciences, University of Miami.

which shrimp were able to swim and which would not disturb the sandy substrate.

On the night preceding each experiment, juvenile shrimp (total length, 6–10 cm) were collected from the ebb tide in a channel within the Everglades estuary of southern Florida, where tides are semidiurnal. They were collected from different times of the lunar cycle, and thus from tides occurring at different times during the night. [This species is only active at night (Hughes, 1968).] From there they were transported immediately to the laboratory and placed in the current chambers. Seven were used at a time during the experiments of series I (Fig. 1), and eight at a time in the experiments of series II (Fig. 2).

During "daylight" hours the shrimp remained buried within the substrate but, after the floodlamp was extinguished in the evening, they all invariably emerged within 20 minutes. Their movements were recorded at intervals from this time until sunrise the following day when the enclosure was again illuminated, and those shrimp, which had not already done so, reburrowed. Movements were recorded in terms of the number of shrimp which passed a vertical mark on the current chamber in either an up or downstream direction during a two minute period. Being a circular chamber, the same animal would often be counted several times during each count period. [The extent of movement with the current per unit of "effort" is obviously greater than movement against the current. Therefore to enable more ready comparison of the two activities, up and downstream movements have been plotted on different scales (Figs. 1 and 2).]

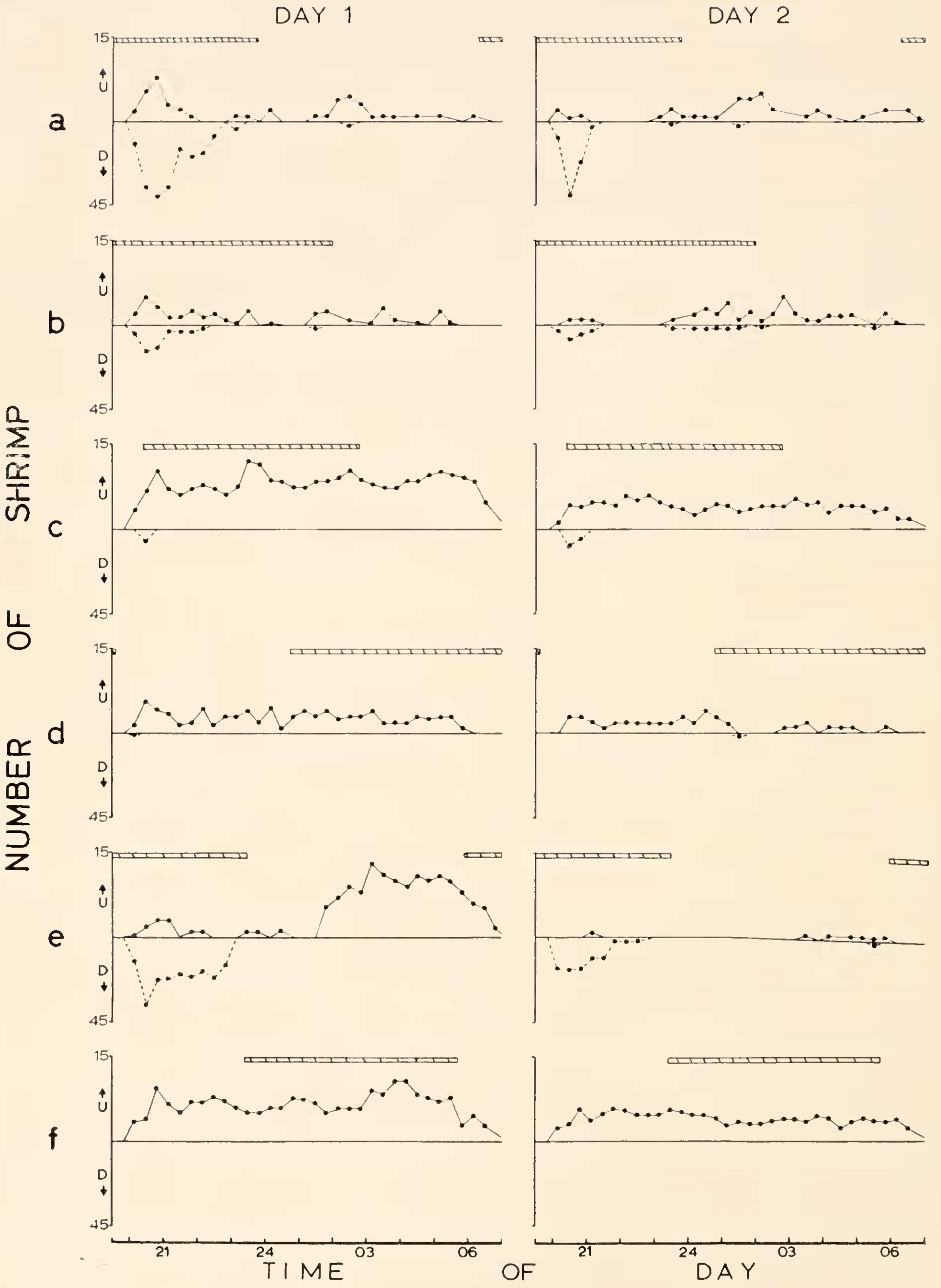
Results

In series I (Fig. 1) only one chamber was used and the movements of the shrimp were recorded on two consecutive nights following their capture. In series II (Fig. 2) similar groups were placed in two identical current chambers and the movements of both groups were recorded on only one night following capture.

A marked synchrony in the activities of all or most individuals was evident from observations of their movements within the current; generally all shrimp within a group would, at the same time, carry out essentially the same type of swimming, in terms of their velocity and direction with respect to current. Although social facilitation may play a role in maintaining this synchrony, observations of the shrimp themselves suggested that such a role was small. At times when direction of swimming with respect to current was reversing, those shrimp which had already changed their direction of swimming had no noticeable effect on others, swimming in the opposite direction, despite frequently colliding with them. Indeed, few external stimuli modified their swimming. If fed during either intense downstream or upstream swimming the shrimp would usually hold and eat the food while continuing to swim in the same direction as before.

Although the results sometimes indicate that both upstream and downstream swimming occurred concurrently, individual shrimp were not in fact continuously swimming in different directions but all or most were swimming upstream, releasing the substrate and drifting downstream before settling and resuming upstream movement.

In addition to the synchrony existing among individuals, the results indicate a similarity between (i) the swimming of a group of shrimp within the current chamber on both the first and second night following its collection from nature


DAY 1
DAY 2
15
U
D
45
a
b
c
d
e
f
NUMBER OF SHRIMP
21
24
03
06
TIME OF DAY

(Fig. 1), and, (ii) the swimming of two groups, collected together but maintained in separate current chambers (Fig. 2).

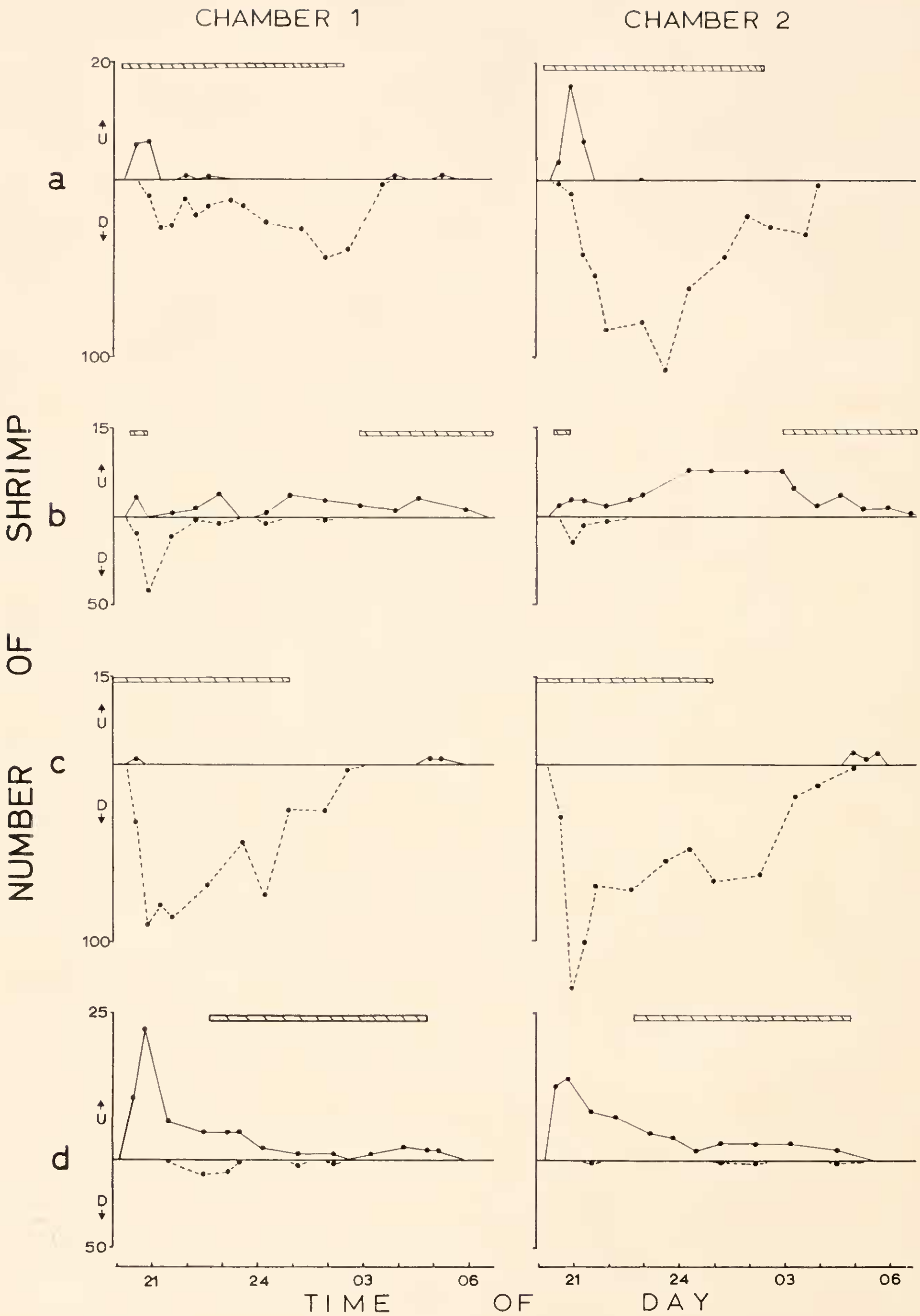
It is also apparent that the general pattern of swimming, especially with regard to its direction, is influenced by the time of the ebb tide from which the shrimp were collected in nature. In this connection a valid generalization appears to be that, those shrimp which, on the day of their collection, emerged from the substrate into an ebbing tide, would, the following day in the current chamber, swim downstream for a period approximating the ebb in nature (Fig. 1a and e; Fig. 2b and c). However, those which emerged into a flooding tide would swim upstream throughout the following night in the current chamber (Fig. 1c, d, and f; Fig. 2d). The behavior of those which emerged into the end of one or the other tide or into the slack water between the tides was more ambiguous (Fig. 1b and c; Fig. 2a).

The relationship between the tide cycle from which the shrimp were collected and their subsequent swimming in the current chamber was investigated on four other occasions, twice with shrimp which had emerged from the substrate into ebb tides and twice with shrimp which had emerged into flood tides. Their swimming during the first few hours of the evening was intermittently observed and each case further confirmed the above generalizations.

Discussion

The sum of these results is evidence that both direction and level of swimming activity is under some measure of endogenous control. The predictable relationship existing between the stage of the tidal cycle in nature and the pattern of swimming in the current chamber suggests that some aspect of the tidal cycle to which the animals were exposed immediately prior to capture, entrains a pattern of swimming which may persist for at least two days in a current, constant in terms of speed and "water quality." From these results the nature of the timing mechanism and its entraining factors is obscure. Salinity changes are, however, suggested as being of possible significance. The direction of swimming of juveniles with respect to current may be directly influenced by their responses to changes in salinity (Hughes, 1969). These changes in salinity and consequent reversals in the direction of swimming occur regularly with change of tide in nature. Earlier experiments indicated that shrimp responded more readily to a salinity decrease imposed at the time of the ebb tide than to one imposed at the time of the flood (Hughes, 1967). This suggested that salinity change was the probable Zeitgeber maintaining the synchrony between the pattern of swimming and the tide cycle. Subsequent experiments were often contradictory and gave no unequivocal indication of a "periodically changing sensitivity of the organism to the stimuli of the Zeitgeber" (Aschoff, 1965, p. 95). It is therefore no longer possible to conclude that salinity change is the entraining factor. In addition, the absence of downstream swimming

Figure 1. The number of shrimp which moved in either an up or downstream direction during observations made at 10 or 20 minute intervals in a current chamber throughout the two nights following their collection from nature. Upstream movement (U) is indicated by the points connected by the unbroken line above the abscissa, and downstream swimming (D) by the broken line below the abscissa. The six pairs of "curves" (a–f) represent the records of shrimp collected less from ebb tides occurring at different times of the night (late summer 1966). The time of the ebb tide on the night of capture is indicated by the transverse bars.


CHAMBER 1
CHAMBER 2
20
100
15
50
15
100
25
50
U
D
a
b
c
d
NUMBER OF SHRIMP
21
24
03
06
TIME OF DAY

in the current chamber, during the time of late night ebb tides, makes any explanation, solely in terms of a tidal rhythm, difficult.

The occurrence of spontaneous reversals in rheotaxis has apparently not been observed before. In this case the reversals were apparently linked adaptively with the tide cycle: downstream swimming in the current chamber occurred only at the time of ebb tides in nature. It did not, however, occur at the time of all ebb tides but only those occurring early in the evening. In nature the response of the shrimp to the salinity decrease accompanying the ebb tide would ensure that shrimp swim downstream (and thus move in an offshore direction) during all ebb tides.

Juvenile penaeids often carry out extensive movements between their inshore "nursery areas" and the offshore waters in which they spawn. There is evidence that they school during these movements and that some cohesion of the aggregations is maintained. This probably ensures that individuals at a similar developmental stage will arrive at spawning sites together and it may confer a measure of protection from predators. The method whereby cohesion is maintained in pink shrimp, especially in view of their nocturnal activity, is not clear. However, the marked similarity of the swimming behavior between groups and its endogenous control, as shown by these results, further supports the contention (Hughes, 1968) that cohesion of aggregations of migrating shrimp may largely be maintained by the control over their activities of various biological timing mechanisms. Indeed, there appears to be no evidence for the presence of any form of social interaction which could similarly serve this purpose.

I would like to thank the Committee for Research and Exploration of the National Geographic Society, Washington, D. C., for their generous support of this project. I also thank Dr. C. P. Idyll, of the Institute of Marine Sciences, University of Miami, for providing facilities within the Division of Fishery Sciences, and Drs. H. Schöne and K. Hoffmann of the Max-Planck-Institut für Verhaltensphysiologie, for their comments on the manuscript.

Summary

1. Evidence that the swimming of migrating juvenile pink shrimp is under some measure of endogenous control was derived from experiments which indicated (i) that the pattern of swimming exhibited by a group of shrimp, maintained under constant conditions within a current of water, was similar over each of the two nights following their collection from nature, and (ii) that the swimming of two such groups, collected together, but maintained in separate current chambers within the laboratory, was similar during the night following their capture.

2. Endogenous control over swimming extended to the sign of rheotaxis which, during certain nights, in the absence of change in external conditions, would reverse in all shrimp at approximately the same time.

FIGURE 2. The number of shrimp in two separate but identical current chambers which moved in either an up or downstream direction during observations made at intervals throughout the night following their collection from nature. The records were repeated on four occasions (a–d) with groups of shrimp collected from ebb tides occurring at different times of the night (mid-summer 1967). For further explanation see Figure 1.

3. A predictable relationship occurred between the tide cycle to which the shrimp were exposed prior to capture and their subsequent swimming in the laboratory. The adaptive nature of this relationship is suggested from the fact that downstream swimming, which in nature occurs only during ebb tides and facilitates the offshore movements of juveniles, occurred in the laboratory only at the time of ebb tides in nature. It did not, however, occur at the time of all ebb tides but only during those occurring early in the evening.

4. It is suggested that the cohesion of the aggregations of migrating shrimp may largely be maintained by means of the synchrony imposed on the activities of all individuals by endogenous timing mechanisms.

LITERATURE CITED

Aschoff, J., 1965. *Circadian clocks.* North-Holland Publishing Co., Amsterdam, 479 pp.

Beauchamp, R. S. A., 1933. Rheotaxis in *Planaria alpina. J. Exp. Biol.* **10**: 113–29.

Beauchamp, R. S. A., 1937. Rate of movement and rheotaxis in *Planaria alpina. J. Exp. Biol.* **14**: 104–16.

Creutzberg, F., 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in tidal areas. *Netherlands J. Sea Res.* **1**: 257–338.

Hughes, D. A., 1967. On the mechanisms underlying tide associated movements of *Penaeus duorarum.* Contribution to the FAO World Scientific Conference on the Biology and Culture of Shrimps and Prawns, Mexico City.

Hughes, D. A., 1968. Factors controlling emergence of pink shrimp (Penaeus duorarum) from the substrate. *Biol. Bull.* **134**: 48–59.

Hughes, D. A., 1969. Responses to salinity change as a tidal transport mechanism of pink shrimp, *Penaeus duorarum. Biol. Bull.* **136**: 43–53.

Keenleyside, M. H. A., and W. S. Hoar, 1954. Effects of temperature on the responses of young salmon to water currents. *Behaviour* **7**: 77–87.